The Taxonomy and Calling Songs of United States Tree Crickets (Orthoptera: Gryllidae: Oecanthinae). I. The Genus *Neoxabea* and the *niveus* and *varicornis* Groups of the Genus *Oecanthus*[1]

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ABSTRACT

The tree crickets of the United States include *Neoxabea bipunctata* (De Geer) and 14 species of *Oecanthus*. The latter are separable into three groups, as follows. (1) the *niveus* group includes *O. niveus* (De Geer), formerly known as *angustipennis* Fitch; *O. exclamationis* Davis; *O.* **leptogrammus,** whose range is from northern South America to southernmost Texas; *O. rileyi* Baker, a West Coast species formerly regarded as a physiological race of the snowy tree cricket; and *O. fultoni,* the well-known snowy tree cricket, misidentified for many years as *O. niveus*. (2) The *varicornis* group includes *O. varicornis* Walker, primarily Mexican but ranging into southeastern Texas; *O. californicus* Saussure, a western species; and *O. latipennis* Riley, confined to the eastern States. These last two species had not been correctly distinguished previously, and are best separated by characteristics of the stridulatory file. (3) The *nigricornis* group, which will be treated in a subsequent publication. *O. discoloratus* Fitch and *O. fuscipes* Fitch are placed as nomina dubia. The first two groups and their respective species are discussed in terms of nomenclature and synonymy, geographic distribution, habitat relationships, seasonal life history, morphology (including characters of the stridulatory file), and calling song. The calling song is a particularly useful taxonomic character because it is directly involved in the maintenance of reproductive isolation among sympatric species. Factors causing intraspecific variation in calling songs are discussed, and the effect of temperature is stressed. The descriptions of calling songs are based on field notes and the analysis of extensive recordings made in the field and under controlled laboratory conditions. For most species data are adequate to show the effect of temperature upon frequency, pulse rate, and (for chirping species) chirp rate.

The Oecanthinae[3] are commonly called "tree crickets" because many of the species are arboreal; however, there are other species which seldom occur in trees but are at home on herbaceous plants. The Oecanthinae are distinguished from all other Gryllidae by their slender bodies, almost horizontal heads, and very slender posterior legs. Of the three genera placed in the subfamily, *Oecanthus* is worldwide in distribution, *Xabea* is found only in Australia and the Malay Archipelago, and *Neoxabea* is restricted to the New World.

The omnivorous food habits of tree crickets have resulted in their being classified as beneficial for their attacks on plant lice, and injurious for their damage to developing flowers and fruit. They also cause damage by ovipositing in the stems of fruit trees and berry bushes and have been implicated in the transmission of a fungus which attacks apple trees.

Most of our present knowledge of the biology and taxonomy of the Oecanthinae of the United States is a result of the careful work of B. B. Fulton (1915, 1925, 1926a, 1926b). His papers serve as a background for this revision, and the reader should refer to them for further details of life history and biology.

Fulton (1926a) recognized eight species of tree crickets as occurring in the United States, and he subdivided one of these species into three subspecies. New information from several sources justifies a considerable revision in Fulton's classification. I recognize 15 species of United States Oecanthinae and discuss 9 of them in this paper. The six species of the *Oecanthus nigricornis* group will be dealt with in a second paper.

METHODS

Examination of Types.—All existing types of United States Oecanthinae were examined except those of *O. formosus* F. Walker (=*Neoxabea bipunctata*), *O. exclamationis* Davis, and *O. nigricornis* F. Walker.

Examination of Collections.—In the course of this study, thousands of specimens were examined from various collections, and data on seasonal and geographical distribution were taken. Certain records of distribution will be substantiated by the use of the

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[1] Portions of this study were supported by grants from the Graduate School of the Ohio State University and from the National Science Foundation (NSF-G13081). Accepted for publication August 3, 1961.

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[3] Some orthopterists (e.g., Chopard 1956) classify the tree crickets as a full family, the Oecanthidae.

following abbreviations: ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania; BBF, B. B. Fulton collection, North Carolina State College, Raleigh; CAS, California Academy of Sciences, San Francisco; CIS, California Insect Survey, University of California, Berkeley; LACM, Los Angeles County Museum, Los Angeles, California; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; OSM, Ohio State Museum, Columbus; OSU, Department of Zoology and Entomology, Ohio State University, Columbus; TJW, author's collection; UA, Department of Entomology, University of Arizona, Tucson; UCLA, Department of Entomology, University of California, Los Angeles; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, U. S. National Museum, Washington, D. C.

Use of Characters of the Stridulatory File.—The structure of the stridulatory file provides reliable characteristics for separating certain species which are otherwise difficult to distinguish. The file was examined by removing the right tegmen of the male and mounting it in Hoyer's medium, ventral surface up, on a microscope slide. The teeth were counted with the aid of a compound microscope, and the length of the file was measured from the mesal surface of the knob, which is at the lateral end of the file, to the mesal edge of the last file tooth. The file is usually gently curved at one or both ends, but the length was determined along a straight line parallel to the central portion of the file. After study the tegmen was usually mounted on a card point on the same pin as the rest of the specimen.

Use of Calling Songs.—The males of all tree crickets produce characteristic calling songs which attract sexually responsive females of the same species. Differences in calling songs are therefore important as isolating mechanisms among sympatric species. The nature of the calling song is a means of determining with certainty most species of tree crickets. In several cases it is the most reliable way to distinguish between closely related species. The value of the calling song in the taxonomy of singing Orthoptera was pointed out by Fulton in his 1931 paper on *Nemobius,* and had been noted previously to some extent by him and other workers. However, two recent developments have greatly enhanced the study of orthopteran sounds and their relationship to classification. First, the development of magnetic tape recording and machine analysis of sounds has made possible the accurate and objective study of orthopteran sounds. With such methods, sounds produced at different times and in different places are readily compared. Features of the song which escape analysis by human ear are easily detected. Second, the repeated demonstration of the role of the calling song in bringing the sexes together has established that differences in calling songs are involved in the maintenance of reproductive isolation between species (e.g., Walker 1957). Such a relationship provides a rational basis for considering certain calling song differences of particular taxonomic significance. R. D. Alexander has been particularly active in the use of modern techniques in studying orthopteran acoustics and in stressing the taxonomic significance of such studies. His work on *Gryllus* (1957a) and *Nemobius* (partly in conjunction with E. S. Thomas; see Thomas and Alexander 1957, Alexander 1957b, Alexander and Thomas 1959) has demonstrated the fruitfulness of this approach when correlated with studies of morphology, ecology, and seasonal and geographical distributions.

The recordings used in this study were made at a tape speed of 15 inches per second. In the field, Magnemite 610E recorders were used, while in the laboratory, PT6 and PT63 Magnecorders were used. Recorded sounds were analyzed with either a Vibralyzer or a Sonagraph (both made by Kay Electric Co., Pine Brook, New Jersey).

Most of the tapes used in this study are in the Laboratory for the Study of Animal Sounds, Department of Zoology and Entomology, The Ohio State University, Columbus, and the remainder are in the tape library of The Department of Entomology, University of Florida, Gainesville, Florida.

If the calling song is to be of use in discriminating between species, an understanding of the variation in calling song *within* a species is essential. The principal source of intraspecific variation in tree cricket calling songs is the effect of temperature. At lower temperatures the individuals of a given species move their wings more slowly in stridulating than they do at higher temperatures. When the wings are moved more slowly, the *pulse rate* (each pulse corresponds to a wing stroke) and pitch of the song decrease. In those species that group their pulses into "chirps", the rate of chirping is also reduced.

The importance of this temperature effect is clear when one considers that the principal difference between the calling songs of some species is the pulse rate. Although pulse rate is characteristic for a given species at a given temperature, individuals of two species singing at different temperatures may have identical pulse rates. Furthermore, I have demonstrated (Walker 1957) that in most species of tree crickets the response of females to songs of their own species and lack of response to those of other species is dependent upon differential response to pulse rates rather than to other features of the song. Only in those species which group their pulses into uniform chirps is pulse rate of no apparent significance, and here the evidence points toward the chirp rate being important.

Since pulse rate (and chirp rate, if any) varies with temperature within each species of tree cricket, an adequate description of the calling song must include the relationship between temperature and pulse rate (and chirp rate, if any). I have repeatedly recorded under controlled temperatures the songs of 9 of the 15 species of United States tree crickets. Constant temperatures from 60° to 100° F. were used, and the air temperature immediately around the cricket was determined after each recording. The analysis of these recordings revealed the relation between temperature and pulse rate for each of the nine species. In three other species enough recordings were made in the field under varying temperatures to give a reasonable indication of the temperature-pulse-rate relation.

Differences in frequency[4] of tree-cricket songs seem to have no significance in the response of the female (Walker 1957), but when considered with pulse rate, frequency may be of some value to the taxonomist in the separation of species. The relation between frequency and pulse rate (and hence temperature) within a species is more variable than is the relation between pulse rate and temperature. Figure 1 shows the frequency of the calling song plotted against the pulse rate in *Oecanthus fultoni.* The amount of variation is typical of the other species studied.

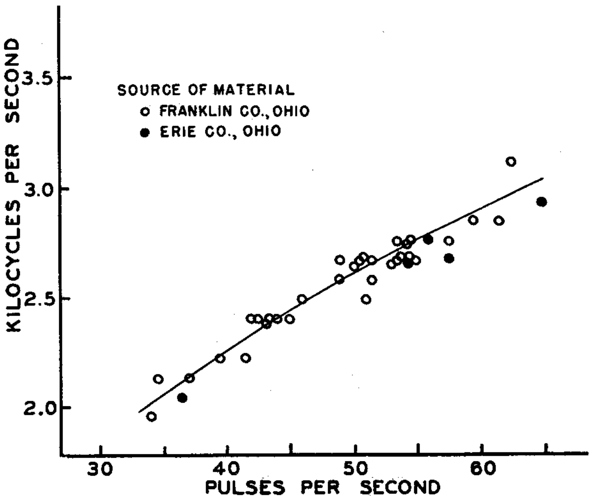

FIG. 1.—Relationship between pulse rate and frequency in *Oecanthus fultoni,* laboratory recordings. Curve fitted by eye.

Since temperature has such a pronounced effect upon the nature of tree-cricket calling songs, the question arises as to whether other extrinsic factors, such as humidity and wind, have an influence.

Fulton (1925) and Allard (1930a) found no correlation between humidity and chirp rate in *Oecanthus fultoni.* In laboratory experiments with *O. fultoni, O. nigricornis,* and *O. quadripunctatus,* I could establish no effects on pulse rate with relative humidities of about 10% and 90% at approximately 75° F. (Walker 1962). Allard (1930b) reported a slight increase in the chirp rate of *O. fultoni* when the singing cricket was exposed to air currents; however, I repeated this experiment with negative results (Walker 1962). In addition, no effect of wind on pulse rate was found in *O. fultoni, O. nigricornis,* or *O. latipennis.*

If these or other extrinsic factors (other than temperature) influence the pulse rate or chirp rate of tree-cricket calling songs, the effects must be less than that of individual differences.

Individual differences account for much of the scattering of points evident in the figures showing effect of temperature on pulse rate. Whenever songs of several individuals of the same species were recorded under a variety of conditions, consistent differences among individuals were discovered. For example, figure 2 shows the relationship of pulse rate to temperature in laboratory recordings of two individuals each of *O. argentinus* and *O. quadripunctatus.* These two cases were selected because the differences are unusually large.

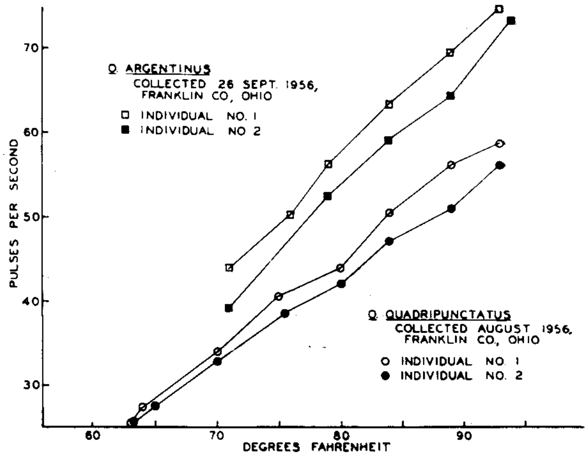

FIG. 2.—Effect of individual variation upon temperature-pulse-rate relationships. These examples were selected because they exhibit *maximum* differences.

Age and fatigue were investigated as possible sources of variation in pulse rate with negative results (Walker 1962). Summer and fall generations of *O. argentinus* showed no consistent differences in calling song. Geographical variation in calling song is surprisingly minor and will be considered in the taxonomic section.

KEY TO UNITED STATES OECANTHINAE

The following key is a summary of the characters which are most useful in identifying both living and preserved specimens. Members of the *Oecanthus nigricornis* group key out to the appropriate group but not to species. A key to the species of this group will be included in a second paper.

1\. Distal portion of hind tibiae armed with several long spines and many shorter ones; first antennal segment frequently marked with black ventrally and without a prominent tubercle on distal border................*Oecanthus* 2

1'. Hind tibiae armed with terminal spurs only; first antennal segment not marked with black ventrally, and with a small prominent tubercle on distal border...*Neoxabea bipunctata* (De Geer)

2(1). Inner edge of ventral face of first antennal

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[4] In descriptions of sounds, *frequency* is the number of cycles per unit time and is expressed in cycles (or kilocycles) per second. *Pitch* is a subjective property which varies with frequency.

segment with a pale swelling marked with black; stridulatory file with fewer than 30 teeth per mm. of length; calling song a broken trill or regular chirp........***niveus*** group 3

2'. Inner edge of ventral face of first antennal segment without a pale swelling; stridulatory file frequently with more than 30 teeth per mm. of length; calling song a continuous trill 7

3(2). Black mark on first antennal segment round or oval (occasionally a second black mark near distal border of segment); second antennal segment usually with a similar mark; width of dorsal field of male tegmina more than four-tenths of length; more than 35 teeth in stridulatory file; calling song a regular chirp 4

3'. Black mark on first antennal segment neither round nor oval; second segment with an elongate black mark; width of dorsal field of male tegmina frequently less than four-tenths of length; less than 35 teeth in stridulatory file; calling song a broken trill.......................... 5

4(3). Occurring only in far western states (perhaps only in California, Oregon, and Washington); song at 70° F. about 90 chirps per minute; eggs laid in compact rows, usually in small diameter stems with the eggs all slanting across the pith; dark mark on second antennal segment usually reduced (length much less than half length of segment) or absent, center of mark near distal border of segment ....***O. rileyi*** Baker

4'. Occurring throughout most of the United States including the far western states; song at 70° F. at least 120 chirps per minute; eggs laid singly, usually in the bark of trees. *In the far western states,* song at 70° F. at least 150 chirps per minute, dark mark on second antennal segment usually at least half the length of the segment, center of mark near midpoint of length of segment.......................... ....***O. fultoni*** n. sp.

5(3'). Disk of pronotum at least one-third longer than wide; black mark on first antennal segment straight and of uniform width; known in the United States only from Cameron County, Texas................***O. leptogrammus*** n. sp.

5'. Disk of pronotum not much longer than wide; black mark on first antennal segment curved or slightly enlarged proximally; widely distributed 6

6(5'). Mark on first antennal segment straight (rarely slightly curved); no prominent orange markings on vertex; length of male tegmina 12-15 mm.; file teeth more widely spaced (19-23.4 teeth per mm.)......***O. exclamationis*** Davis

6'. Mark on first antennal segment strongly curved toward the inner side or J-shaped; vertex yellow or orange (in fresh specimens); length of male tegmina 9.8-12.2 mm.; file teeth less widely spaced (23.7-29.7 teeth per mm.)..............................***O. niveus*** (De Geer)

7(2'). First antennal segment unmarked with black, or with a narrow dark line along inner edge; frons and basal segments of antennae usually tinged with red; width of dorsal field of male tegmina about half of length; subgenital plate of female with a broad notch posteriorly, one-fourth to one-half as broad as widest part of plate............***latipennis*** group 8

7'. First antennal segment often marked with more than a single black line; head and antennae not tinged with red; width of dorsal field of male tegmina rarely over four-tenths of length; subgenital plate of female with a narrow notch posteriorly, not more than one-fifth as broad as widest part of plate........... ....***nigricornis*** group

8(7). Third segment of antenna usually much darker than the second; frequently a distinct dark line on inner edge of first two antennal segments; depression in distal portion of terminal segment of maxillary palp usually more than one-half the length of the segment; length of male tegmina usually less than 14 mm.; stridulatory file with 29–38 teeth per mm. 9

8'. Third segment of antenna seldom darker than the second; no distinct dark line on inner edge of first two antennal segments; depression in distal portion of terminal segment of maxillary palp usually less than four-tenths the length of the segment; length of male tegmina usually more than 14 mm.; stridulatory file with 27-31 teeth per mm................ ....***O. latipennis*** Riley

9(8). Stridulatory file 0.86-1.20 mm. long with 26-36 teeth; known in the United States only from southeast Texas............***O. varicornis*** F. Walker

9'. Stridulatory file 1.20-1.85 mm. long with 40-58 teeth; occurs throughout western U. S. ....***O. californicus*** Saussure

Neoxabea Kirby, 1906:76

The sole United States species of *Neoxabea* is *bipunctata,* which is the type of the genus by monotypy.

Neoxabea bipunctata (De Geer)

The Two-Spotted Tree Cricket, Figs. 3, 4, and 5

Gryllus bipunctatus De Geer, 1773, p. 523 (type locality, Pennsylvania; type, a female in the De Geer Collection, Natrhistoriska Riksmuseum, Stockholm, Sweden).
Oecanthus bipunctatus (De Geer) Serville, 1831, p. 135.
Xabea bipunctata (De Geer) Riley, 1881, p. 61.
Neoxabea bipunctata (De Geer) Kirby, 1906, p. 76.
Acheta punctulatus, Gmelin, 1788, p. 2063 (erroneous subsequent spelling of *bipunctatus*).
Oecanthus punctulatus, Fitch, 1856, p. 415 (erroneous subsequent spelling of *bipunctatus*).
Oecanthus formosus F. Walker, 1869, p. 94 (type locality, Mexico; type, a female in the British Museum, London, England).

Oecanthus formosus Walker is listed as a synonym of *N. bipunctata* because Kirby (1906), who had the holotype at hand, placed it as such. Walker's description of *formosus* definitely places it in *Neoxabea,* and nothing in the description prevents it from being *bipunctata.*

DISTRIBUTION.—The distribution of *bipunctata* (fig. 3) corresponds approximately with the deciduous forest region of eastern North America. The species has been reported from Vera Cruz, Mexico (Rehn 1902), and from Nicaragua (Baker 1905), but another species might be involved. Peripheral records for the United States are as follows: TEXAS, Brownsville (OSU), Victoria (USNM), Dallas (MCZ); KANSAS, Morris Co. (BBF); IOWA, Story Co. (Froeschner 1954); WISCONSIN, Richland Co. (USNM); MICHIGAN, Ann Arbor (UMMZ); MASSACHUSETTS, Holliston (MCZ); FLORIDA, Liberty Co. and Alachua Co. (UMMZ).

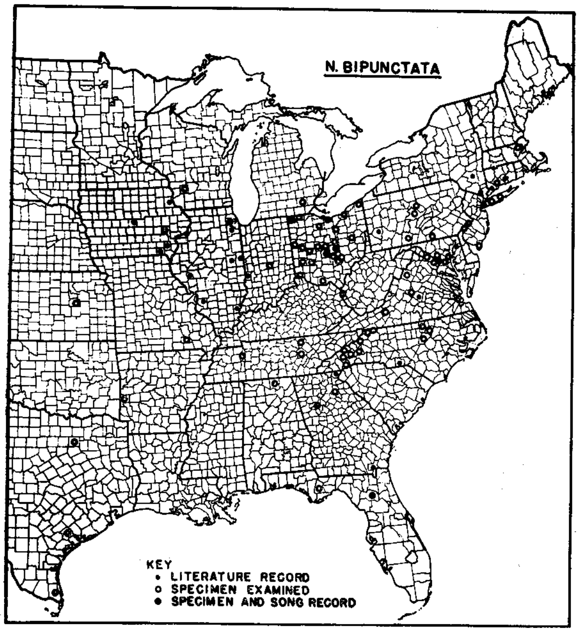

FIG. 3.—Geographical distribution of *Neoxabea bipunctata* in the United States.

ECOLOGY.—*N. bipunctata* occurs on deciduous trees and in tangled undergrowth. It is often collected on wild grape vines and has been found in such trees as apple, wild cherry, ash, elm, oak, sugar maple, hackberry, willow, and sassafras. In central Ohio the first adults appear at the end of July, and some individuals evidently live until frost. In the southern part of its range adults have been collected as early as May 8 (Brownsville, Texas) and June 5 (Gainesville, Florida), but none has been collected in these States later than August 22. There is thus no evidence of more than one generation per year.

CALLING SONG.—The calling song of *N. bipunctata* may be termed a *broken trill.* A pulse sequence of uniform pulse rate is discontinued and begun at irregular intervals of from one to several seconds. Two other eastern species, *Oecanthus niveus* and *O. exclamationis,* are known to produce broken trills, and it is difficult to separate their songs by ear from that of *N. bipunctata.* All three sing from trees and vines, chiefly at night. In general, *N. bipunctata* and *O. exclamationis* interrupt their songs less frequently than does *O. niveus.* These first two species often trill 10 seconds or longer before pausing briefly, while *O. niveus* seldom trills more than 5 seconds at a time and may have more pronounced pauses between trills. A complicating factor is that all three species sing more irregularly when they are disturbed or are just beginning to sing.

Analysis of recordings of *bipunctata* reveals that the calling song can be readily separated from those of *exclamationis* and *niveus* on the basis of pulse rate. At any given temperature *bipunctata* has by far the highest pulse rate of any tree cricket song studied. Figure 4 shows the relation between temperature and pulse rate as indicated by five field recordings. No laboratory recordings were obtained although five adult males were kept in the laboratory for over a month. Field recordings definitely assignable to *bipunctata* were difficult to obtain because individuals usually sang from perches out of reach.

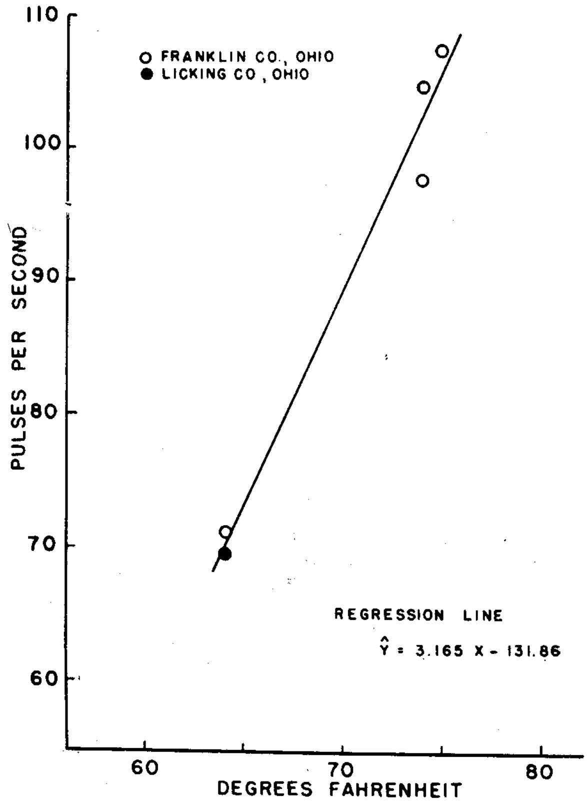

FIG. 4.—Effect of temperature on pulse rate in *Neoxabea bipunctata*, field recordings.

The relationship between frequency and pulse rate is very similar for *bipunctata* and *exclamationis* but will usually separate the songs of *bipunctata* and *niveus* (fig. 5).

Oecanthus Serville, 1831:134

OECANTHUS NIVEUS GROUP

The *niveus* group is characterized by a broad swelling on the inner edge of the ventral face of the first antennal segment. The area between the eyes is frequently tinged with yellow, and the file teeth are spaced more widely than in other groups. The calling song is either a *regular chirp,* i.e., the pulse sequence is broken into approximately uniform bursts with uniform intervals, or a broken trill. It is produced chiefly at night. There are five United States species in the *niveus* group; two of these previously have had no valid name.

Oecanthus niveus (De Geer)

The Narrow-Winged Tree Cricket, Figs. 5, 6, 7, 8

Gryllus niveus De Geer, 1773, p. 522 (type locality,

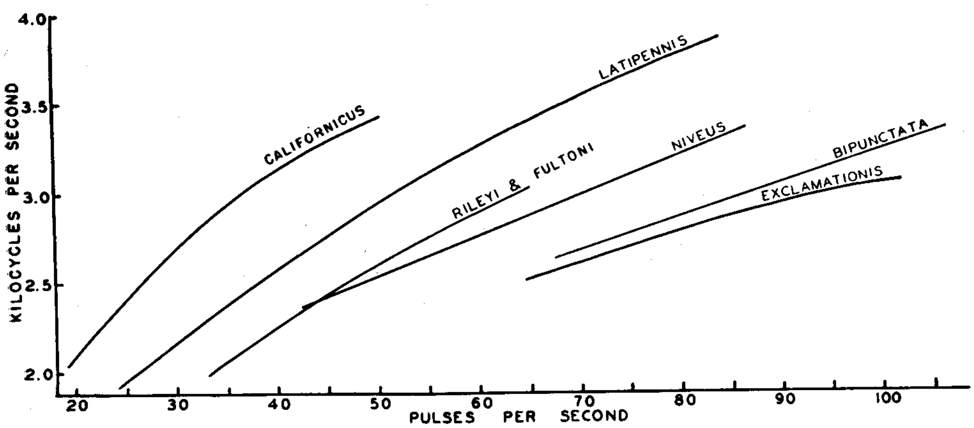

FIG. 5.—Relationship between pulse rate and frequency in seven species of tree crickets. Each curve was drawn by eye from a scatter diagram similar to figure 1.

Pennsylvania, female lectotype here designated from three syntypes in the De Geer Collection, Naturhistoriska Riksmuseum, Stockholm, Sweden).
Oecanthus niveus (De Geer) Serville, 1831, p. 135.
Oecanthus niveus var. *g. angustipennis* Fitch, 1856, p. 413 (type locality, New York; type, a male destroyed).
Oecanthus angustipennis Fitch. Walker, 1869, p. 116.

At present the name *Oecanthus niveus* is widely used for the snowy tree cricket (*Oecanthus fultoni*), but examination of the type material by the author revealed that the name must be applied to the narrow-winged tree cricket instead. The former name of the narrow-winged tree cricket, *Oecanthus angustipennis* Fitch, was therefore placed as a junior synonym of *niveus* in a recent paper by Walker and Gurney (1960).

De Geer's type series of *niveus* consists of three females—all are definitely narrow-winged tree crickets. Dr. René Malaise of the Riksmuseum is sure that they are the specimens, and the only specimens, used by De Geer in preparing his description (personal communication).

The misuse of the name *niveus* is a result of failure to consult the type material, the original description being insufficient to place the species accurately. In 1841, Harris described what he thought was *niveus* as possessing "a minute black dot on the under sides of the first and second joints of the antennae." In the eastern United States these dots are peculiar to the snowy tree cricket. Later authors seem to have accepted Harris's erroneous concept of *niveus* without question, although some authors prior to 1900 lumped several species (always including *fultoni*) under the name *niveus* (e.g., Scudder 1862).

The name *angustipennis* needs some discussion even though it is a secondary synonym of *niveus*. In 1856, Fitch published a lengthy commentary on the "White Flower-Cricket, *Oecanthus niveus*, Degeer." Under this label Fitch evidently included all U. S. Oecanthinae he had seen except *Oecanthus nigricornis* (which he called *fasciatus*) and *Neoxabea bipunctata* (which he called *Oecanthus punctulatus*). The species Fitch thought was typical *niveus* was actually *fultoni*. Fitch concluded his description of *"niveus"* (actually *fultoni* plus other species) by describing seven "varieties". He designated four of these varieties with a letter only (*a, b, c,* and *d*). He gave Latin names in addition to letters to the other three varieties—*"e. discoloratus," "f. fuscipes"* and *"g. angustipennis."*

Fitch's description of *angustipennis* was too general to identify the species he had; however, the name became attached to the narrow-winged tree cricket (Davis 1889, Hart 1892), and finally Beutenmüller (1894) concluded that since Fitch's types of *Oecanthus* "have been destroyed" and correct identification can never be ascertained, *angustipennis* should "be retained for the species so well known to us by this name."

Fitch's *angustipennis* is thus fixed as a secondary subjective synonym of De Geer's *niveus*. The disposition of Fitch's other two named varieties is not so easy. Both *discoloratus* and *fuscipes* were cited as species by F. Walker in 1869, but no other author has cited them as such. Fitch's description of *discoloratus* reads, "The whole of the head, the first joint of the antennae, the breast and abdomen of a brownish clay color." Any specimen of a tree cricket which had been stained with fluids from other specimens or which had been left in a killing jar overnight could fit this description. Fitch's description of *fuscipes* reads, "One or both the hind legs more or less tinged with blackish." *O. nigricornis* is the only species in New York which ordinarily has blackish hind tibiae, but Fitch placed specimens of *nigricornis* in his *fasciatus*. Melanistic individuals are known in other species; for instance, Allard (1929) found a "black or melanistic individual of the snowy-tree cricket chirping in the usual manner near Washington, D. C." Fitch's specimens of *fuscipes* could well have been slightly melanistic individuals of any species of *Oecanthus* occurring in New York.

Since neither name can be placed definitely on the basis of Fitch's description and since the types have been destroyed, *discoloratus* and *fuscipes* should be considered *nomina dubia* (new designation) and be unavailable.

Oecanthus exclamationis Davis

Davis's Tree Cricket, Figs. 5, 6, 7, 8

Oecanthus exclamationis Davis, 1907, p. 173 (type locality, Staten Island and New Jersey; types, 4 female syntypes at the Staten Island Institute of Arts and Sciences, Staten Island, New York).

I. C. G. Cooper, Curator of the Davis Collection, Staten Island Institute of Arts and Sciences wrote (personal communication) that there are four specimens of *exclamationis* in the collection marked "Co-Type." All are females, there being one each from Staten Island; Cranford, New Jersey; Farmingdale, New Jersey; and Manasquan, New Jersey.

Oecanthus leptogrammus, new species

Thin-Lined Tree Cricket, Figs. 6, 7

This species has been identified as *O. varicornis* by some authors, but the original description of *varicornis* precludes the use of that name for this species (see p. 317). *O. leptogrammus* is distinct from other members of the *niveus* group in its very thin longitudinal lines on the basal segments of the antennae (fig. 7c) and in its slender head and pronotum. It is named *leptogrammus* (*leptos*—thin; *gramme*—line) because of its antennal markings.

Holotype: Male; Brownsville, Cameron County, Texas, 23 May 1913. Type No. 5,830, Academy of Natural Sciences of Philadelphia. Background color like that of *O. niveus* (dried specimens). Head slender, no orange on top. Basal segment of antenna with longitudinal swelling on inner edge of ventral face. This swelling marked with thin dark brown line 0.02 mm. wide and 0.22 mm. long. Second antennal segment with slight ventral swelling marked with a shorter but similar line 0.02 mm. wide and 0.14 mm. long. Remainder of specimen without prominent markings. Sensory area on terminal segment of maxillary palpus slightly more than half length of segment.

Allotypic Female: Same data and disposition as holotype except collected July 31-August 5, 1912, by Hebard. Color and markings as in holotype except antennal markings narrower and tibial spines tipped with dark brown.

Measurements of Holotype and Allotype (in millimeters): Length of body, ♂, 13.4, ♀, 12.7; length of pronotum, ♂, 2.8, ♀, 2.6; caudal width of pronotal disk, ♂, 2.0, ♀, 1.8; length of tegmen, ♂, 12.6, ♀, 12.1; greatest terminal width, ♂, 5.3, ♀, 2.6; length of hind femur, ♂, 8.5; ♀, 8.5; length of ovipositor, 4.0.

Paratypes: 13 ♂♂, 17 ♀♀, 2 juveniles, as follows:

Academy of Natural Sciences of Philadelphia (7) —TEXAS: Brownsville, Cameron Co., 31 July–5 Aug. 1912, Hebard, 1 ♂, 2 ♀♀, 1 juv. S. Tex. Garden, Brownsville, 21 Nov. 1910, 1 ♀. Piper Plantation, near Brownsville, 3 Aug. 1912, Rehn and Hebard, 1 ♀, 1 juv.

U. S. National Museum (10)—TEXAS: Esperanza Ranch, Brownsville, May, 3 ♂♂, 1 ♀; September, 1 ♀; no date, 1 ♀. Brownsville, 6 Oct. 1904, H. S. Barber, 1 ♀. MEXICO: Cordova, May, L. O. Howard, 1 ♂. PANAMA: E. Bethel, 1 ♂. Barro Colorado Island, Canal Zone, 24 Jan. 1940, James Zetek, 1 ♀.

University of Michigan Museum of Zoology (15) —MEXICO: Tamaulipas, 18 mi. N. E. Victoria, Rio Corona, xero-mesic woodland along river, 17 Dec. 1941, Cantrall and Friauf, 1 ♀. Tamaulipas, 17 mi. N. Victoria, Rio Santa Engracia, tall herbaceous and shrub growth covering flood plain margins, 28 Dec. 1941, Cantrall and Friauf, 1 ♀. Tamaulipas, 8 mi. E. Padilla, Rancho Santa Ana, xeric woodland along river, Cantrall and Friauf, 19 Dec. 1941, 1 ♂, 1 ♀; 22 Dec. 1941, 1 ♂, 1 ♀; 24 Dec. 1941, 1 ♀. San Luis Potosi, Tamazunchale, 22 Aug. 1954, F. N. Young, 1 ♂. GUATEMALA: Petén, Poptún, 6′-10′ up in small broad-leaved shrubs growing in understory of open pine woods, 15 Apr. 1956, Hubbell and Cantrall, 2 ♂♂, 1 ♀. Petén, Tikal, 21 Feb. 1956, shrub in quasi-rain-forest, I. J. Cantrall, 1 ♀. Petén, Tikal, thicket surrounding pond in quasi-rain-forest, 16 May 1956, T. H. Hubbell, by beating, 1 ♀. HONDURAS: El Paraiso, Choluteca Bridge, Tegucigalpa-Danli Road, 1,950′, foliage of tree in gallery forest, 25 July 1948, T. H. Hubbell, by beating, 1 ♂. COLOMBIA: Vista Nieve, Sierra Nevada de Santa Marta Mts., 5,200′, at light, 6 Aug. 1926, F. W. Walker, 1 ♂.

Oecanthus rileyi Baker

Riley's Tree Cricket, Figs. 5, 6, 7, 11, 13

Oecanthus rileyi Baker, 1905, p. 81 (type locality, mountains near Claremont, California; type, a male in the Pomona College Collection, Claremont, California).

Oecanthus niveus Fulton (*not* De Geer), 1925, p. 365 (race "B").

O. rileyi and the following species, *O. fultoni,* were first differentiated by Fulton (1925), who considered them "physiological varieties" of the snowy tree cricket. He described their distinctive songs and egg laying habits but did not call them distinct species since he could find no morphological differences. The fact that colonies of the two forms exist in close contact (sometimes in the same bush or tree) with no indication of interbreeding justifies considering them distinct species.

Oecanthus fultoni, new species

Snowy Tree Cricket, Figs. 1, 5, 6, 7, 9, 10, 11, 12, 13

Oecanthus niveus, Harris (*not* De Geer, 1773), 1841, p. 124.

This is the species which has long been wrongly identified as *niveus.* It is named in honor of the late Dr. B. B. Fulton, who contributed more than any other worker to our knowledge of the biology and classification of tree crickets.

Holotype: Male; Franklin County, Ohio, 21 July 1955, T. J. Walker, collector. Deposited at University of Michigan Museum of Zoology. Background color like that of *O. niveus.* Top of head between eyes and antennae orange yellow. Basal segment of antenna pale orange yellow except for prominent swelling on inner edge of ventral face. This swelling white and marked with black spot 0.12 mm. in diameter. Second antennal segment with slight ventral swelling marked with black ellipse 0.14 mm. long and 0.09 mm. wide. Except for dark tips of tibial spines, remainder of cricket without prominent markings. Sensory area on terminal segment of maxillary palpus slightly more than half length of segment.

Allotypic Female: Same data and disposition as holotype. Color and markings as in holotype.

Measurements of Holotype and Allotype (in millimeters): Length of body, ♂, 12.3, ♀, 9.2; length of pronotum, ♂, 2.2, ♀, 2.2; caudal width of pronotal disk, ♂, 2.0, ♀, 2.1; length of tegmen, ♂, 12.7, ♀, 11.2; greatest tegminal width, ♂, 5.9, ♀, 2.8; length of hind femur, ♂, 7.8, ♀, 7.6; length of ovipositor, 4.0.

Paratypes: Since the snowy tree cricket is perhaps the best known U. S. species, no paratypes are designated.

DISTRIBUTIONAL RELATIONSHIPS IN THE *niveus* GROUP

Figure 6 shows the geographic distribution of the five species of the *niveus* group.

O. niveus and *exclamationis* are principally inhabitants of the deciduous forest areas of eastern United States. A series of *exclamationis* from the Huachuca Mountains of southeastern Arizona makes the distributional pattern of this species different from those of all others. One of this series has antennal markings (but not other traits) which suggest *O. niveus,* and a record of Scudder and Cockerell (1902) of *niveus* from southern New Mexico may therefore refer to *exclamationis* instead. Neither *niveus* nor *exclamationis* are known from outside the United States. Peripheral records for *niveus* are as follows: TEXAS, Kerrville (ANSP); OKLAHOMA, Carter Co. (UMMZ); KANSAS, Wichita (USNM); NEBRASKA, Omaha (UA); SOUTH DAKOTA, Yankton (Hebard 1925); MINNESOTA, no specific locality (Lugger 1897); MICHIGAN, Isabella and Midland Counties (UMMZ); NEW YORK, Niagara Co. (CAS), Wayne Co. (USNM); MASSACHUSETTS, Hampshire and Middlesex Counties (USNM); FLORIDA, Marco, Collier Co. (TJW). Peripheral records for *exclamationis* are as follows: ARIZONA, Cochise Co., Carr Canyon, Huachuca Mts., 8-9 Aug. 1952, H. B. Leech and J. W. Green, 1 ♂ (CAS), Aug. 1905, H. Skinner, 4 ♂♂, 1 ♀ (ANSP), 16 Oct. 1905, M. Hebard, 1 ♂ (ANSP); Cochise Co., Reef, 3 Nov. 1903, 2 ♂ (ANSP), no date, Biederman coll., 1 ♀ (ANSP); Santa Cruz Co., Santa Rita Mts., 18 Aug. 1935, E. I. Beamer, 1 juv. (ANSP); LOUISIANA, Rapides Parish (TJW); ARKANSAS, Polk Co. (ANSP); OKLAHOMA, Noble Co. (ANSP); IOWA, Henry Co. (UMMZ); MICHIGAN, Charlevoix Co. (USNM); NEW YORK, Ithaca (USNM), Ulster Co. (personal communication from Fred Hough); CONNECTICUT, New Haven (ANSP); FLORIDA, Volusia and Orange Counties (UMMZ).

O. leptogrammus is known to occur in the United States only in Cameron County, Texas. Its occurrence elsewhere is detailed in the list of paratypes.

The limits of distribution of *rileyi* are uncertain because of the difficulty in distinguishing pinned specimens from those of *fultoni.* The morphological characters which serve to separate California specimens of *rileyi* and *fultoni* may not apply to all populations of these species. The records indicated in figure 6 are those which seem conclusive. Certainly the song records are reliable. Some specimens from outside this range have morphological traits similar to *rileyi,* but additional information is necessary before their status is certain. These specimens indicate a possible extension of the range of *rileyi* into Idaho, western Nevada, southern Arizona, and southwestern New Mexico. The peripheral records indicated in figure 6 are as follows: WASHINGTON, Pullman (UMMZ); CALIFORNIA, Riverside Co. (UCLA); Los Angeles Co., Catalina Island (LACM). All song records are by the author except those for Santa Clara Co., California (Smith 1930), and Benton Co., Oregon (Fulton 1925).

O. fultoni occurs throughout the United States except in the southeast. Its distribution in the far west is poorly known because of confusion with *rileyi.* Except for the song records, the records of *fultoni* in Idaho, Utah, and Arizona (fig. 6) are largely based on the assumption that *rileyi* does not extend eastward into these states. The occurrence of *fultoni* in southwestern Idaho is substantiated by Wakeland's (1927) description of the egg-laying habits. Peripheral U. S. records of *fultoni* are as follows: CALIFORNIA, San Diego Co., Alpine (CAS); OREGON, Benton Co. (Fulton 1925); WASHINGTON, Walla Walla Co. (UMMZ); IDAHO, Adams Co. (Wakeland 1927); SOUTH DAKOTA, Lawrence Co. (Hebard 1925); MINNESOTA, no specific locality (Lugger 1897); WISCONSIN, Trempealeau Co. (USNM); Fond du Lac Co. (Hebard 1934); MICHIGAN, Midland and Huron Counties (UMMZ); VERMONT, Lamoille Co. (USNM); MAINE, Portland (Morse 1920); NORTH CAROLINA, Hoke Co. (TJW); GEORGIA, Jackson Co. (Allard 1910); ALABAMA, Cleburne Co. (UMMZ); TENNESSEE, Lawrence Co. (UMMZ); ARKANSAS, Yell Co. (UMMZ); TEXAS, Harrison Co., song heard by TJW. In addition to its distribution in the United States, *fultoni* is known from Ontario, Canada (Walker 1904), and Tamaulipas, Mexico (UMMZ).

HABITAT RELATIONSHIPS

Both *niveus* and *exclamationis* are characteristic of the crowns of deciduous trees. *O. exclamationis* is the more strictly arboreal of the two and has been collected from apple, oaks, elm, hackberry, catalpa, wild cherry, and maples. It sometimes occurs in understory trees and in tangled undergrowth. *O.*

niveus is found in the same habitats as *exclamationis* but also occasionally occurs on herbaceous plants. For instance, it has been found on cocklebur and blackberry, on goldenrod (Davis 1914), and on ironweed (Blatchley 1903).

I have no data as to the habitat of *leptogrammus* in the United States. The collection data given for the paratypes from Mexico, Honduras, and Guatemala, indicate that it inhabits woody plants in a wide variety of situations.

In the eastern United States, *fultoni* is common in shrubbery and vines about houses, in unsprayed fruit trees, and in the tangles of vines and trees that grow in neglected fence rows and at the edges of clearings. It is sometimes numerous on blackberry. In wooded areas it is not so common in the crowns of tall trees as *niveus* and *exclamationis*, but is more often in low trees and shrubby undergrowth. The southeastern-most records are from low oaks. In the western United States, *fultoni* is especially

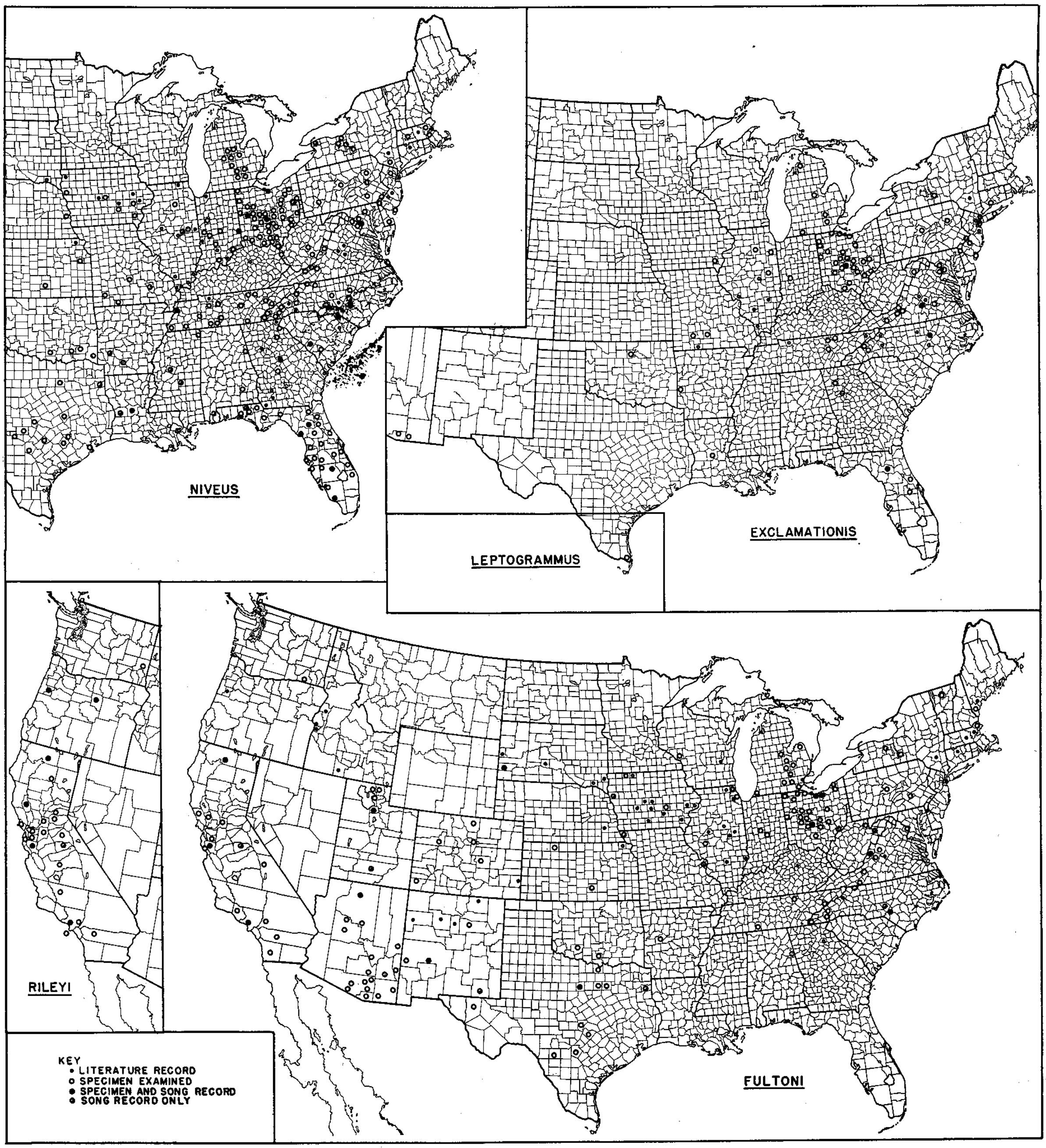

FIG. 6.—Geographical distribution of the species of the *Oecanthus niveus* group. Only records from the United States are indicated.

characteristic of scrub oaks, but also occupies taller broad-leaved trees where these occur. In Idaho it has been so numerous on prune trees as to be a serious pest (Wakeland 1927).

Fulton (1925) described *O. rileyi* in eastern Oregon as principally a bush-inhabiting form. He found it especially common on loganberry, raspberry, and wild rose and also noted it among brake ferns and associated plants in old burned areas. In the same region Fulton found *fultoni* to be strictly arboreal, and most common in prune, apple, ash, and oak. The only berry bushes he found *fultoni* in were growing under trees.

Smith (1930) reported *rileyi* as a major pest of commercial raspberries in the Santa Clara Valley of California. He also found *fultoni* in the same raspberry patches but in much smaller numbers.

On a trip in August 1959, I observed *rileyi* in five areas, and in three of these *fultoni* was also found. In Yosemite Valley, California, *rileyi* was heard in the vines which covered a building. *O. fultoni* was heard in large numbers in apple trees in an old orchard, and a few were in tall oaks. In Siskiyou County, California, both *rileyi* and *fultoni* were common in a chaparral. There was no apparent difference in their habitats, groups of each species being scattered throughout the area. *O. rileyi* was slightly more abundant on the basis of a count of singing males. In Beverly Hills and the nearby University of California at Los Angeles campus, *rileyi* and *fultoni* were abundant and showed only slight differences in habitat preferences. *O. rileyi* was heard singing from vines, shrubbery, low trees, and in the crowns of high trees. *O. fultoni* was heard in the same type of places, but was more frequent in arboreal situations while *rileyi* was slightly more common in lower, shrubby vegetation. The two species were not usually found in the same tree, bush, or vine, but occasionally they were. For instance, both species were collected in the same vine (*rileyi* in larger numbers) and in the same *Hibiscus* hedge (*fultoni* in larger numbers). The areas in which only *rileyi* was observed were in Lake County, California and Wheeler County, Oregon. In the former locality, *rileyi* was found in a weedy area with no trees and was also heard fifteen feet up in a large oak; in Wheeler County, it was collected in dense weeds near a creek.

SEASONAL LIFE HISTORY

In central Ohio, *exclamationis* matures about the first of August and is heard until mid-October. There is no evidence of a second generation in any part of its range, but the data are too scanty to be decisive. In central Ohio, *niveus* has a life cycle like that of *exclamationis*; however, in the southern part of its range, *niveus* has at least two generations per year. At Gainesville, Florida, in 1960, the first generation of adults appeared in mid-May and an abundance of late-instar nymphs in early September indicated a fall generation. Farther south in Florida, adults have been collected in all months except February and April.

O. fultoni and *O. rileyi* evidently have but one generation per year throughout their ranges. *O. fultoni* in central Ohio matures about the middle of July, and some individuals live until killed by late October frosts. In a study of *O. rileyi* in the Santa Clara Valley of California, Smith (1930) reported adults as early as June 28 and as late as November 21.

The seasonal life history of *O. leptogrammus* is not known. Adults have been collected in Cameron County, Texas, as early as May 23 and as late as November 21.

MORPHOLOGICAL CHARACTERS

The dark marks on the first two antennal segments are the easiest means of distinguishing most of the United States species of the *niveus* group (fig. 7 and the key on p. 306).

The separation of *fultoni* and *rileyi* on the basis of antennal markings is based principally on the examination of 11 specimens of *fultoni* (all from California —Los Angeles, 10; Siskiyou Co., 1) and 19 specimens of *rileyi* (18 from California—Los Angeles, 12; Lake Co., 3; Siskiyou Co., 3; and 1 from Wheeler Co., Oregon). These specimens are in the author's collection and were the only ones of positive identity available from the area in which both species occur. All specimens of *rileyi* examined, except one, had the mark on the second antennal segment much reduced or absent. The exception was the specimen (identified as *rileyi* by song) collected in Wheeler Co., Oregon. In this case the mark was as large as in *fultoni*, but it was still confined to the distal half of the segment (fig. 7I). In all *fultoni* examined, except one, the mark on the second antennal segment was more than half the length of the segment. The exceptional specimen was from Siskiyou Co., Calif., and had a much reduced mark; however, the center of the mark lay near the midpoint of the length of the segment instead of near the distal border. Of 115 additional specimens examined from the area of overlap, 78 were easily placed as *rileyi* on the basis of the antennal markings, 32 as *fultoni*, and only 5 could not be identified as either with certainty. In specimens east of the known range of *rileyi* the antennal characters of *fultoni* are usually like those of far-western *fultoni*. In no case is the second antennal mark reduced to the extent common in *rileyi*. However, some specimens have the mark principally in the distal half of the segment and would be placed in *rileyi* if they came from California. Specimens of this type are especially numerous from southern Arizona and southwestern New Mexico and frequently have file characters (see below) suggestive of *rileyi*. These specimens may represent morphological variants of *fultoni* or an eastward extension of the range of *rileyi*.

The antennal markings of specimens of *fultoni* from eastern Texas and southern Oklahoma are fre-

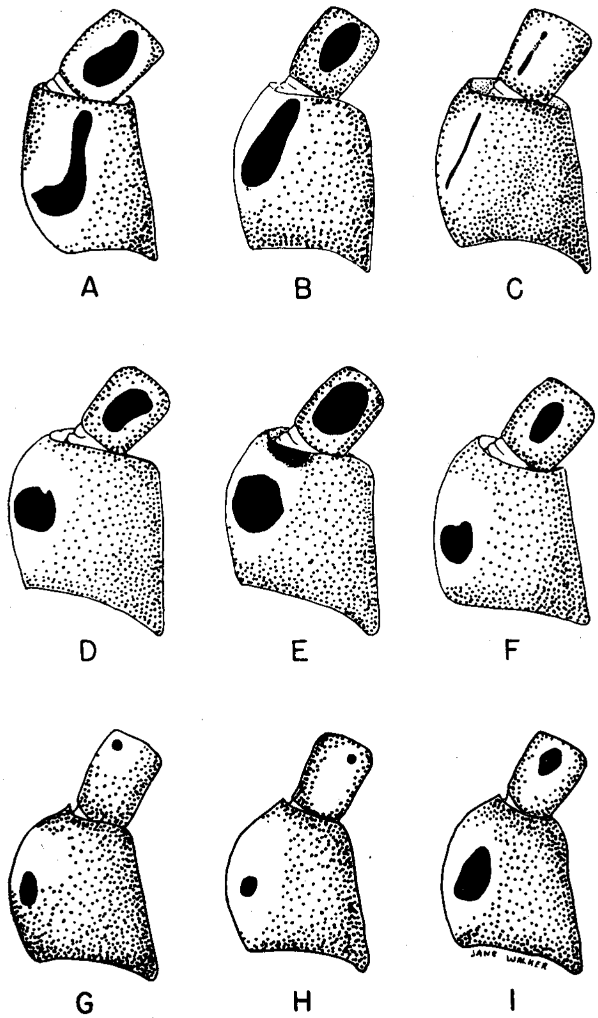

FIG. 7.—Antennal markings of the *Oecanthus niveus* group. A. *niveus*; B. *exclamationis*; C. *leptogrammus*, holotype; D. *fultoni*, holotype; E. *fultoni*, Palo Pinto County, Texas; F. *fultoni*, Los Angeles County, California; G. *rileyi*, holotype; H. *rileyi*, Los Angeles County, California; I. *rileyi*, Wheeler Co., Oregon.

quently unique in having *two* dark marks on the first antennal segment. In addition to the usual mark, there is a mark near the distal edge (fig. 7E).

Another trait of value in the *niveus* group is the color of the vertex. In fresh specimens of *fultoni* the vertex is usually orange or orange yellow. In fresh specimens of *rileyi* the vertex has no orange or is faintly tinted with orange. This same color trait is of use in separating *niveus* (orange) from *exclamationis* (no orange). Unfortunately the color fades as specimens age.

The characteristics of the stridulatory file (table 1) are of use in separating some species of the *niveus* group. In California, *rileyi* and *fultoni* differ in the average spacing of the file teeth, *rileyi* (16 specimens) having 22.8-25.8 teeth per mm. and *fultoni* (10 specimens) having 25.5-29.2 teeth per mm. The fact that the type of *rileyi* had 24.3 teeth per mm. (42 teeth in 1.73 mm.) was one factor in placing its name with the present species and not with the species here called *fultoni*. There is an important complication in the use of file characteristics in distinguishing *rileyi* and *fultoni*. In the eastern United States, *fultoni* has a *lower* average number of teeth per mm. than does *rileyi* in California. Since *fultoni* in California has a higher average number of teeth per mm. than *rileyi*, it is obvious that the file characters of *fultoni* show geographic variation. As a matter of fact specimens of *fultoni* from Utah, Colorado, Arizona, New Mexico, and Texas tend to have the spacing of the file teeth intermediate between far-western and eastern specimens, i.e. similar to California *rileyi*.

Another pair of species which may be separated by file characters is *niveus* and *exclamationis*. Although these two are usually easily separated by the antennal markings, one specimen from southeast Arizona had markings of an intermediate nature. The other twelve specimens from the same area were marked like typical *exclamationis*. Examination of the file traits revealed that all specimens were like eastern *exclamationis*. On this basis literature records of *niveus* in the southwest must be questioned.

Table 1.—Characteristics of the stridulatory file.

Species	Localities	Sample size	No. of teeth		Length (mm.)		Teeth per mm.	
			Range	Mean	Range	Mean	Range	Mean
N. bipunctata	Ohio	6	20-23	21.5	0.85-1.04	0.94	21.2-24.7	23.0
O. niveus group								
niveus	10 states	20	22-30	26.0	0.88-1.13	1.00	23.7-29.7	25.8
exclamationis	7 states	16	17-23	20.5	0.86-1.08	0.97	19.0-23.4	21.1
leptogrammus	6 countries	12	21-32	28.3	0.91-1.30	1.14	21.1-29.2	24.8
rileyi	California	16	38-46	42.6	1.59-1.84	1.75	22.8-25.8	24.3
fultoni	California	10	40-47	43.9	1.49-1.77	1.64	25.5-29.2	26.8
fultoni	eastern U. S.	20	38-45	41.3	1.57-2.02	1.79	21.8-25.3	23.0
O. varicornis group								
varicornis	Texas & Mexico	24	26-36	33.0	0.86-1.20	1.06	29.0-35.2	31.3
californicus	8 states	46	40-58	47.5	1.20-1.85	1.44	29.5-37.4	33.0
latipennis	7 states	15	36-47	42.1	1.32-1.68	1.48	27.3-30.5	28.4

CALLING SONGS

The calling songs of *niveus, exclamationis,* and *leptogrammus* are broken trills similar to that of *N. bipunctata.*

The song of *leptogrammus* is known only from field notes made by I. J. Cantrall and J. J. Friauf in Tamaulipas, Mexico, and by I. J. Cantrall and T. H. Hubbell in Petén, Guatemala. In each case the song is described as similar to that of *niveus.* The Guatemalan description reads, "Single, fairly loud, low-pitched note, about a second long, like *angustipennis* [*niveus*]." It may be noted that the characteristics of the stridulatory file of *leptogrammus* show a close resemblance to those of *niveus* (table 1).

As discussed under *bipunctata,* the songs of *bipunctata, niveus,* and *exclamationis* are difficult to distinguish by ear; however, analysis of recordings shows marked differences in pulse rate. Figure 8 shows the relationship of temperature and pulse rate in laboratory recordings of *niveus* and *exclamationis.* Field recordings of *niveus* from Ohio, Indiana, Texas, Louisiana, Arkansas, Tennessee, Mississippi, Georgia, South Carolina, and Florida agree reasonably well with the regression line of figure 8. However, the recordings from the southern states seem to have a slightly slower pulse rate than those from Ohio and Indiana. Field recordings of *exclamationis* from Ohio, Virginia, North Carolina, and Florida agree perfectly with the line shown for that species in figure 8.

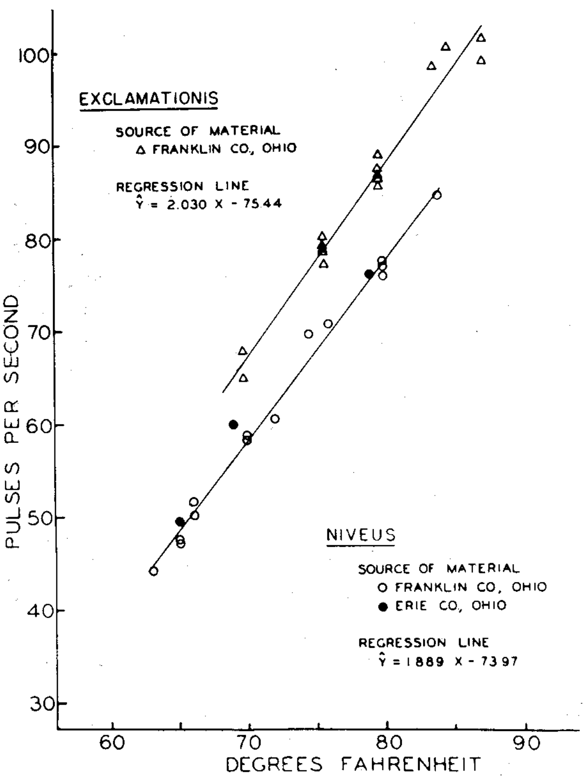

FIG. 8.—Effect of temperature on pulse rate in *Oecanthus exclamationis* and *O. niveus,* laboratory recordings.

O. fultoni and *rileyi* are the only species of U. S. tree crickets that produce a regular chirp (i.e., chirps of approximately uniform duration separated by approximately uniform intervals). Individuals of the same species chirping in the vicinity of one another synchronize their songs. Thus the crickets in a given tree or bush usually chirp in unison producing a throbbing, musical chorus.

The detailed descriptions of the songs of *fultoni* and *rileyi* are more involved than in other species because the number of pulses per chirp and the chirp rate must be dealt with in addition to the pulse rate.

In *fultoni* the chirps usually consist of eight pulses (produced by eight wing strokes) but chirps of five pulses are also common. Chirps of other pulse numbers are only rarely produced and then usually by individuals in discontinuous song. Individuals often produce nothing but 8-pulse chirps for minutes at a time. In some cases there is a regular alternation between 5- and 8-pulse chirps for several hundred chirps.

A count of the pulses in the first 50 chirps in 76 recordings of 40 individuals of *fultoni* gave the following figures—8-pulse chirps, 75%; 5-pulse chirps, 13%; 7-pulse chirps, 7%; 6-pulse chirps 2%. Chirps of no other pulse number constituted as much as 1% of the sample. The recordings represent localities throughout the range of *fultoni* with the exception of the northeastern United States. No geographical variation in pulse number was apparent.

The timing of pulses within the chirp is usually not entirely uniform—each chirp ordinarily begins with a group of two pulses closely followed by consecutive groups of three (fig. 9). Thus the eight-pulse chirp consists of two pulses followed by two sets of three, and a five-pulse chirp is two followed by one set of three. Chirps of other than 2, 5, 8, or 11 pulses usually are the result of pulses being dropped or added to the terminal group of three. This peculiar grouping of pulses within the chirp is much more pronounced in some recordings than in others, but seems always to occur. The reason for the grouping

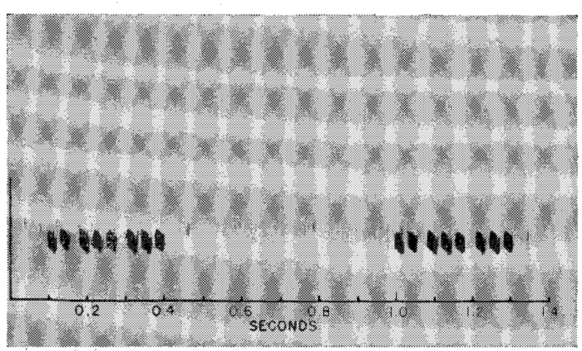

FIG. 9.—Audiospectrograph of two chirps of *Oecanthus fultoni,* showing grouping of pulses within the chirp. University of Florida Recording No. 585-5, 12½° C, Socorro County, New Mexico.

is not known, and the grouping is evidently of no behavioral significance (Walker 1957).

In *rileyi* the chirps usually consist of 11 pulses, although chirps of 8 and 14 pulses are also common. A pulse count of 131 chirps in recordings of four California individuals gave the following figures: 11-pulse chirps, 76%; 8-pulse chirps, 10%; 14-pulse chirps, 9%; 13-pulse chirps, 4%; 10-pulse chirps, 1%. The pulses are grouped within the chirp in the same manner as in *fultoni*—a 14-pulse chirp, for instance, consists of a group of two pulses followed by four groups of three.

An observation made by Fulton (1925, p. 374) in Oregon bears interpretation in the light of these data. On the basis of listening to individuals singing at low temperatures, Fulton concluded that *rileyi* made four wing strokes per chirp and *fultoni* three. Fulton may have been counting the pulse *groups* within the chirp rather than the pulses themselves. If this is the case, *rileyi* was producing 11-pulse chirps and *fultoni* was producing 8-pulse chirps, as is typical for the two species.

The pulse rate in the songs of *fultoni* and *rileyi* is more difficult to measure than in species with broken or continuous trills. The pulse rate that is homologous to that measured in the songs of trilling species is probably the rate during delivery of each of the pulse groups within the chirp. However, this rate is impractical to determine since the entire chirp usually lasts less than 0.3 second. The method used in this study was to determine the time elapsed from the beginning of the second pulse to the beginning of the last pulse in a chirp and to calculate the pulse rate from this datum. In other words the average pulse rate within a chirp is essentially what was considered the pulse rate in these two species.

The pulse rate of *fultoni* (fig. 10) varies with temperature as in trilling species. Western *fultoni* may have a slightly higher pulse rate than Ohio *fultoni*, but the evidence is not conclusive (fig. 11). The pulse rate of *rileyi* is known from only four recordings, all made in the field in California (fig. 11). Comparison of the pulse rates of these recordings with those of recordings of *fultoni* made at the same time shows that at a given temperature *rileyi* has a slightly lower pulse rate than *fultoni*.

The relation between pulse rate and frequency is approximately the same in *rileyi* and *fultoni* (fig. 5).

The ease with which the chirp rate of *fultoni* can be correlated with temperature has led to its being called the "thermometer cricket." Figure 12 shows this correlation as exhibited by Ohio specimens singing under laboratory conditions. Field observations fall along the same line. It follows from these data that a reasonable approximation of the temperature (in degrees Fahrenheit) could be made by counting the number of chirps in 13 seconds and adding 40. A number of other workers have previously noted the relationship of chirp rate and temperature in their localities—Brooks 1882, New England; Dolbear 1897, New England; Bessey and Bessey 1898, Lincoln, Nebraska; Edes 1899, New England; Fulton 1925, Iowa and Oregon; Allard 1930a, Washington, D. C.; Matthews 1942, Detroit, Michigan. Allard (1930a) gave a detailed review of previous work, and such a review will not be repeated here. However, geographical variation in chirp rate will be discussed.

Fulton (1925) concluded that at a given temperature the chirp rate of U. S. *fultoni* tended to increase

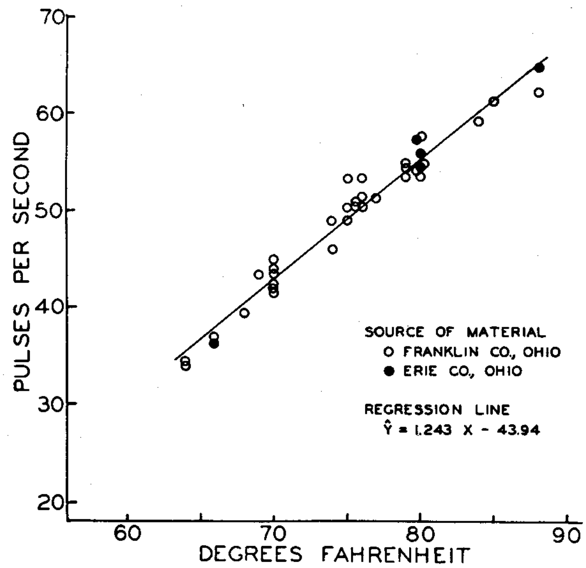

FIG. 10.—Effect of temperature on pulse rate in *Oecanthus fultoni*, laboratory recordings.

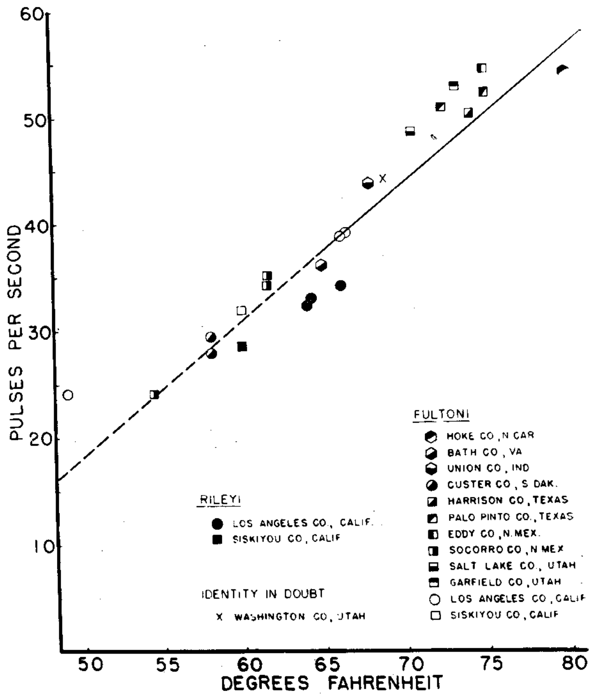

FIG. 11.—Effect of temperature on pulse rate in *Oecanthus rileyi* and *O. fultoni*, field recordings. Line is the regression line for laboratory recordings of Ohio *fultoni* (fig. 10); dotted portion is extrapolated.

from east to west. He found that *fultoni* from New England and Ohio were the slowest chirpers; those from Iowa, Colorado, and Arizona, were somewhat faster; and those from Oregon were faster yet.

In the present study, the data on geographical variation in the chirp rate of *fultoni* agree reasonably well with Fulton's results. Throughout the deciduous forest region of eastern United States the chirp rate seems to be approximately that shown in figure 12. The only observations which conflict with this surmise are those of Brooks (1882) and Dolbear (1897). Each of these workers give a formula relating chirp rate and temperature which would indicate a slower chirp rate at a given temperature than that determined

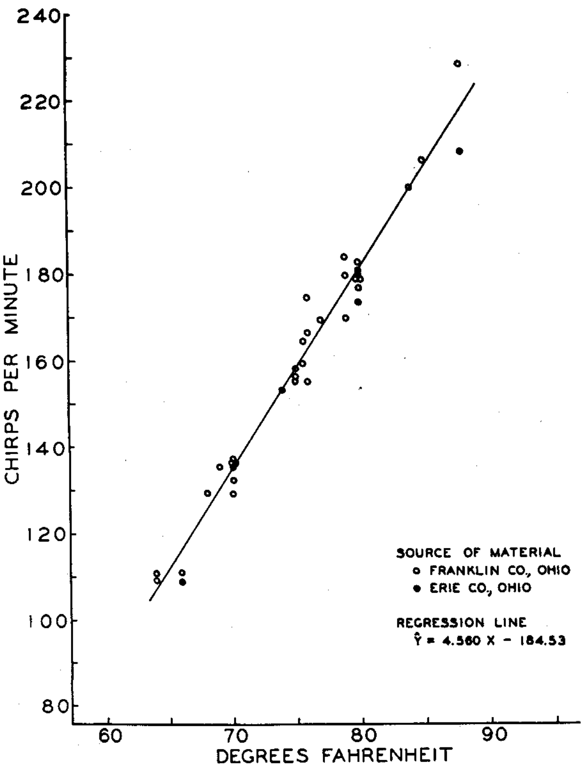

FIG. 12.—Effect of temperature on chirp rate in *Oecanthus fultoni*, laboratory recordings.

by later workers. Since neither worker gives detailed data and since Edes (1899) and Faxon (*in* Edes 1899) do, and they show different results in the same region, it seems proper to doubt the accuracy of the earlier work.

The few observations that Fulton made in the mountain states suggested that here the chirp rate was intermediate between eastern and far western *fultoni*. However, the data collected in the present study do not support this conclusion. Figure 13 shows that *fultoni* from New Mexico and Utah seem to have as fast a chirp rate as Oregon or California *fultoni*. It seems then that east of the Great Plains *fultoni* chirps slightly more slowly than west of the Great Plains, but that within these two areas there

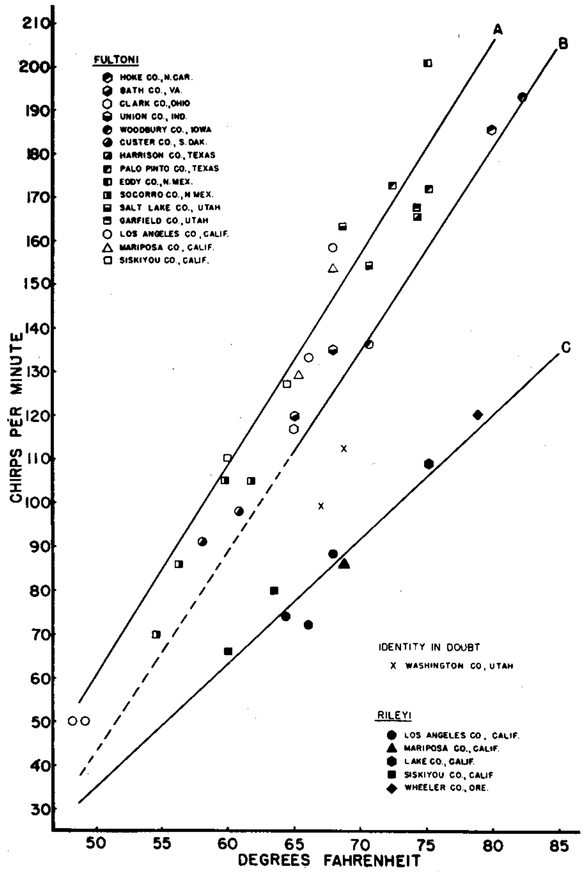

FIG. 13.—Effect of temperature on chirp rate in *Oecanthus rileyi* and *O. fultoni*, field notes and recordings. Line A represents Fulton's (1925) data for Oregon *fultoni*. Line B is the regression line for laboratory recordings of Ohio *fultoni* (fig. 12); the dotted portion is extrapolated. Line C represents Fulton's (1925) data for Oregon *rileyi*.

is little orderly variation in chirp rate.

Two observations of chirp rate made in Zion National Park, Washington County, Utah, do not fit in with other data on chirp rate (fig. 13). These specimens were singing about 20 feet up in a box elder, and none was collected. On the basis of the song the specimens seem more likely to be *rileyi* than *fultoni*. Not only is the chirp rate much slower than *fultoni* from nearby Garfield County, but the majority of chirps contained 11 pulses, typical of *rileyi*, instead of eight, which is typical of *fultoni*. If these specimens were *rileyi*, they extend the known range of the species a considerable distance eastward. It was mentioned in the discussion of morphological characters that some specimens from New Mexico and Arizona are suggestive of *rileyi*.

It should be noted that the chirp rates of *rileyi* and *fultoni* are drastically different, especially in the region in which their ranges are known to overlap. On the other hand differences in pulse rate are very slight. This is not unexpected in view of evidence (Walker 1957) that in *fultoni* the chirp rhythm is of greater behavioral significance to the females than is the pulse rhythm.

DISCUSSION

Comparison of the species within the *niveus* group reveals that *fultoni* and *rileyi* form one subgroup and *niveus* and *exclamationis* another, while *leptogrammus* stands alone, although a little closer to *niveus* and *exclamationis* than to *fultoni* and *rileyi*.

The morphological type represented by *fultoni* and *rileyi* extends throughout Mexico and into Central America and the West Indies. In the West Indies the species is *allardi* (Walker and Gurney 1960), and in Mexico and Central America one or several undescribed species may occur. As far as known, all produce a calling song which is a regular chirp.

It seems probable that *rileyi* developed from a geographically isolated population similar to *fultoni*. After the ranges of the two came to overlap, there was an impetus toward differentiation of calling songs and, to a lesser extent, habitat. This resulted in the rapid evolution of the much slower chirp rate and somewhat different habitat range of *rileyi*. The larger population of the *fultoni*-like species probably showed little change, although the slightly higher chirp rate of *fultoni* in the West is likely a result of the interaction.

Niveus and *exclamationis* are morphologically similar and occupy similar habitats. Their ranges are largely overlapping although *exclamationis* extends into the southwestern states to the seeming exclusion of *niveus*. The occurrence of *niveus*-like antennal markings among the few specimens of *exclamationis* available from the Southwest suggests that the disjunct southwestern *exclamationis* may be similar to the population that differentiated into modern *exclamationis* and *niveus*.

OECANTHUS VARICORNIS Group

In the *varicornis* group there is no swelling on the inner edge of the first antennal segment. The vertex and basal segments of the antennae are usually colored with red or pink. The width of the dorsal field of the male tegmen is about half its length, and the spacing of the file teeth is intermediate between the *niveus* group and most members of the *nigricornis* group. The subgenital plate of the female is broadly notched. The calling song is a continuous trill, produced chiefly at night.

Three U. S. species are here recognized.

Oecanthus varicornis F. Walker

The Different-Horned Tree Cricket, Figs. 14, 15

Oecanthus varicornis F. Walker, 1869, p. 94 (type locality, Mexico; type, a male, lost or destroyed).
Oecanthus marcosensis Baker, 1905, p. 81 (type locality, San Marcos, Nicaragua; type, a male without head or thorax, Pomona College Collection, Claremont, California).

Although *varicornis* was originally described in *Catalogue of the Specimens of Dermaptera Saltatoria . . . in the Collection of the British Museum,* David R. Ragge, Department of Entomology, British Museum, wrote (personal communication), "Unfortunately the type material of *Oecanthus varicornis . . .* has never been in our collection here . . . . I should imagine that this material is now lost or destroyed; if it still exists I cannot imagine where it might be."

Fortunately the original description of *varicornis* permits recognition of the species. The key portions of the description state that the antennae are "black towards the base, testaceous at the base," that the tegmina are "very broad", and that the "colour of the antennae and the broader fore wings distinguish this species from *O. niveus* [=*fultoni* and *allardi*]." The species here recognized as *varicornis* is the only species known from Mexico which fully agrees with Walker's description.

Unfortunately the name *varicornis* has been mistakenly applied to the species here described as *leptogrammus*. Saussure (1874, 1897) was originally responsible for the misidentification, and Rehn (1904) and others perpetuated the mistake. In *leptogrammus* no portion of the antennae is black, and the tegmina are proportionally narrower than *fultoni* rather than wider.

The type of *marcosensis* lacks the head and thorax, but its tegmina resemble those of *varicornis*. Two other specimens from Nicaragua determined as *marcosensis* by Baker substantiate this placement. There is of course the possibility that the Nicaragua specimens belong to a species similar to but distinct from *varicornis*.

Oecanthus californicus Saussure

The Western Tree Cricket, Figs. 5, 14, 15, 17

Oecanthus californicus Saussure, 1874, p. 462 (type locality, California; type, a male in the Muséum d'Histoire Naturelle, Genève, Switzerland).
Oecanthus californicus pictipennis Hebard, 1935, p. 78 (type locality, Rancho del Monte, Santa Fe County, New Mexico; type, a male, 11 Aug. 1934, 7000 ft., Hebard Collection, Type No. 1276, Academy of Natural Sciences of Philadelphia).

Hebard described *pictipennis* as a subspecies of *californicus* differing from typical *californicus* only in coloration. Most of the colors mentioned by Hebard fade rapidly in preserved specimens, so it is difficult to place preserved specimens as *pictipennis* or *californicus*. On the basis of the distribution of brown pigment, which does not fade, *pictipennis* occurs in the southern portion of Colorado and Utah, in the northern portion of New Mexico and Arizona, and in southern and central coastal California. Crickets which are intermediate in coloration between *pictipennis* and typical *californicus* (still on the basis of the brown pigment) are common in Oregon and throughout California. Crickets of typical *californicus* coloration occur throughout the range of *californicus*. No new differences have been discovered between crickets with typical coloration and those with *pictipennis* coloration.

It seems then that *californicus* shows geographic variation as to the occurrence of dark forms and as to the proportion of dark to light forms. If *pictipennis* were retained as a subspecies it would logically apply to both dark and light individuals in areas in which both occurred. This was not the intention of Hebard, since he reported finding "typical *californicus*" along with paratypes of *pictipennis* in southern Utah. In the present state of our knowledge of color variation in *californicus*, it seems best to avoid the use of *pictipennis* as a subspecific name.

Oecanthus latipennis Riley

The Broad-Winged Tree Cricket, Figs. 5, 14, 16

Oecanthus latipennis Riley, 1881, p. 61 (type locality, Missouri or Alabama, probably the former; type, a male, 7 Oct. 1877, Type No. 1113, U. S. National Museum).

Riley's description of *latipennis* was based on 15 specimens from Missouri, one male from Alabama, and one male from Columbus, Texas. The Texas specimen had black marks on the lower surface of the basal joints of the antennae and was probably *varicornis*.

The specimen labeled as the type is one of the Missouri specimens or the Alabama specimen, but is not labeled as to locality.

DISTRIBUTIONAL RELATIONSHIPS

Figure 14 shows the U. S. distribution of the three members of the *varicornis* group.

O. varicornis is chiefly a Mexican species and is known in the United States only from the coastal plain of southeast Texas. *O. californicus* occurs throughout most of the western states and must certainly extend into northern Mexico. However, there are no substantiated records outside of the United States. *O. latipennis* is principally an eastern species, but along rivers its distribution extends westward into the prairie states. Its northward distribution is more restricted than most other eastern tree crickets, perhaps because of its slower maturation.

It should be noted that the known ranges of these three species do not overlap although they are nearly contiguous in eastern Texas. If there is overlapping among the ranges, it seems likely that the area of overlap is small.

The records of *varicornis* in the United States are as follows: TEXAS, Caldwell Co., Lockhart State Park (UMMZ); Jackson Co., Ganado (UMMZ); San Patricio Co., Lake Corpus Christi (UMMZ); Duval Co., San Diego (USNM); Hidalgo Co. (OSU, TJW, UMMZ); Cameron Co. (BBF, CAS, OSU, UA, USNM). Peripheral records of *californicus* are these: WASHINGTON, Clark Co. (USNM); IDAHO, Latah Co. (UMMZ); Butte Co. (TJW); UTAH, Uintah Co., Vernal (UMMZ); COLORADO, Larimer Co., Fort Collins (BBF); OKLAHOMA, Murray Co. (UMMZ); TEXAS, Tarrant Co. (USNM); Burnet Co. (UMMZ); Bexar Co., Helotes (UMMZ).

Peripheral records of *latipennis* are these: FLORIDA,

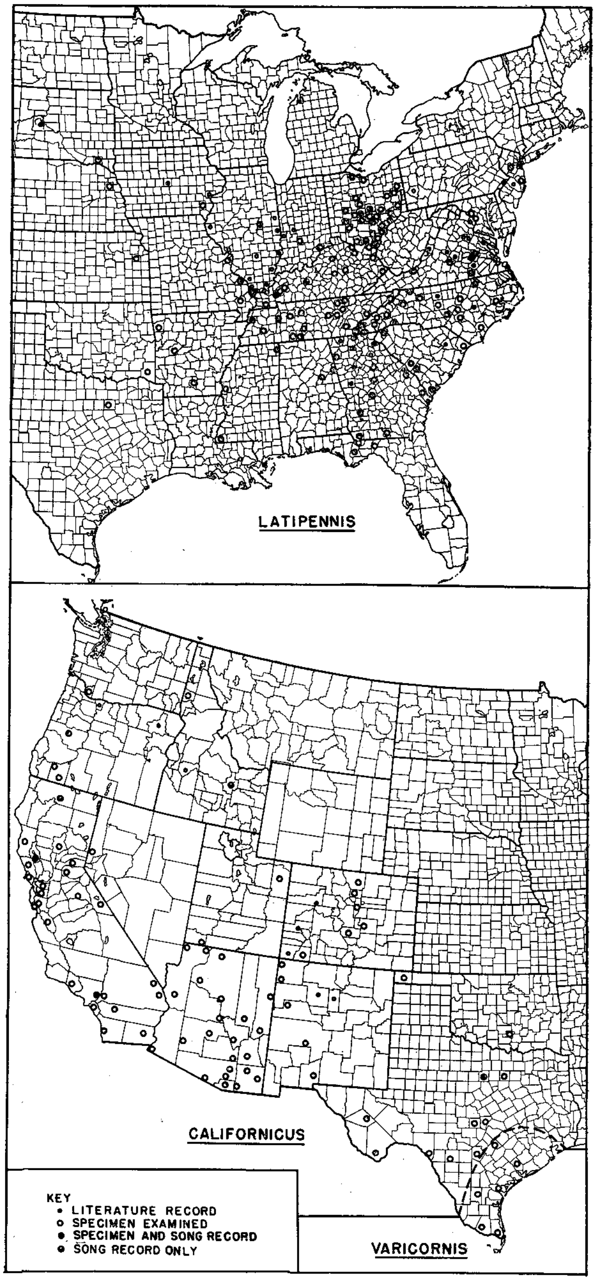

FIG. 14.—Geographical distribution of the species of the *Oecanthus latipennis* group in the United States.

Jefferson, Gadsden, and Liberty Counties (UMMZ); MISSISSIPPI, Wilkinson Co. (UMMZ); TEXAS, Dallas Co., Dallas (UMMZ); OKLAHOMA, McCurtain Co., Eaglestown (UMMZ); KANSAS, Douglas Co. (CAS, CIS); NEBRASKA, Cuming Co. (USNM); SOUTH DAKOTA, Stanley Co., Fort Pierre (Hebard 1925); MINNESOTA, no specific locality (Lugger 1897); MICHIGAN, no specific locality (Fulton 1915); OHIO, Ottawa and Erie Counties (OSM); NEW JERSEY, Somerset Co. (OSM); NEW YORK, Suffolk Co. (Hebard 1925).

HABITAT RELATIONSHIPS

All three members of the *varicornis* group are most often found in areas of scrubby vegetation and are usually seen and heard less than four feet above the ground.

Of the three, least is known of the habitat of *varicornis*. Field notes made by I. J. Cantrall and J. J. Friauf in Texas and Tamaulipas, Mexico, indicate that they collected *varicornis* in scrubby areas containing mesquite and cactus. In Jackson County, Texas, they collected a single male in low herbaceous growth in medium shade beneath scattered live oaks along the Novidad River.

I have collected *californicus* (1) on scrub oak and juniper in north-central Texas, (2) on small spruce-like conifers in a scrubby area in central New Mexico, (3) on piñon in a piñon-joshua tree association at 5,000′ in the San Gabriel mountains of southern California (4) on shrubby oak in the bushy area at 6,500′ in the same mountains, (5) on almond trees and low shrubs in Lake County, California, (6) in chaparral in Siskiyou County, California, and (7) in low scrubby plants on a scrub and grass-covered cinder hillside in Butte County, Idaho. Fulton (1926b) records *californicus* from similar situations in Oregon, northern Arizona, and Banks, Idaho. Near LaGrande, Oregon, he found *californicus* egg punctures in wild rose thickets in mountain-side gullies. Hebard (1929, 1935) found *californicus* on scrub oaks, sage, and a small stiff yucca in Colorado, and in juniper in the juniper-piñon zone of north-central New Mexico.

O. latipennis is often found on shrubs and low trees, particularly scrubby oaks, growing in dry open woods. It is frequently abundant in the thickets of vines, brambles, and coarse weeds that grow along woodland edges, fencerows, and roadsides. Finally, it is sometimes abundant in abandoned fields on coarse weeds such as horseweed, teasel, goldenrod, and blackberry.

SEASONAL LIFE HISTORY

Unlike most other U. S. tree crickets, *varicornis* seems to breed throughout the year. The evidence of this consists of adult specimens from southern Texas collected in every month of the year except July, August, October, and November. Perhaps the lack of a truly cold-hardy stage explains the northward limits of the range of *varicornis*.

O. californicus evidently overwinters only in the egg stage. The earliest date recorded for the adult is May 22 and the latest date is November 29 (both records Pima County, Arizona, UA). There is no clear evidence of more than one generation per year of *californicus* in any part of its range; however, a second generation seems likely in the southern portion of its range. The occurrence of adults over a six-month period is the most convincing indication.

O. latipennis has but one generation per year and is the latest maturing of the eastern tree crickets. In central Ohio the earliest record of an adult is August 14, and in the southern portion of its range there are no records of adults earlier than July 31.

MORPHOLOGICAL CHARACTERS

Specimens of *latipennis* are usually easily distinguished from those of either *varicornis* or *californicus*. Diagnostic characters include the length of a sensory area on the maxilary palp, the coloration of the antennae, and the characteristics of the stridulatory file. These characters are discussed in the following paragraphs.

In all dried specimens of tree crickets there is a longitudinal depression in the distal portion of the terminal segment of the maxillary palp. This depression results from the collapse of what is evidently a sensory area. In specimens preserved in alcohol the area does not collapse, and its extent is sometimes difficult to ascertain. In dried specimens of *latipennis* the depression usually extends proximad less than four-tenths of the total length of the terminal segment, while in *varicornis* and *californicus* the depression usually extends more than one-half the total length of the segment. The maximum proportion recorded for *latipennis* is .44 and the minimum for *varicornis* or *californicus* is .46.

Two features of antennal coloration help set off *latipennis* from *varicornis* and *californicus*. Firstly, the antennae of *latipennis* are suffused with pink, dark red, or purple at the base, and distally the color rapidly fades. The third segment is usually no darker than the second and black pigment is not apparent. In both *varicornis* and *californicus* the first two segments of the antennae are reddish brown. The third segment is usually, but not always, much darker, sometimes jet black. The black pigment rapidly thins distally as does the reddish pigment in *latipennis*. Secondly, the first two antennal segments of *latipennis* never have a distinct dark line on the inner edge of the ventral surface. In *varicornis* and *californicus* they usually, but not always, do.

In overall size, *latipennis* averages considerably larger than either *californicus* or *varicornis;* howvere, the minimum measurements of *latipennis* and the maximum measurements of the other two species (especially *varicornis*) overlap enough to make size of little use in identifying some individuals. For instance, nearly all males of *latipennis* have a tegminal length of more than 14 mm. while in males of *varicornis* and *californicus* the tegminal length is nearly always less than 14 mm. Males with tegmina 13-15 mm. long are not safely identified on the basis of tegminal length.

As to the characteristics of the stridulatory file, males of *latipennis* have a minimum recorded file length of 1.32 mm. while *varicornis* has a maximum of 1.20. Both *varicornis* and *californicus* have the file teeth more closely spaced than in *latipennis*, but there is some overlap (see table 1).

Varicornis and *californicus* are very similar morphologically. The most reliable distinguishing feature discovered is the nature of the stridulatory file. The file of *varicornis* has fewer teeth and is usually shorter than in *californicus* (table 1 and fig. 15). The coloration in the two species shows no consistent differences; however, none of the *varicornis* specimens shows the distinctive pattern of brown pigment found in some *californicus* (as discussed under the name *pictipennis* Hebard). Only one specimen of *varicornis*, from San Patricio County, Texas (UMMZ), shows noticeable areas of brown pigment, and these are not at all conspicuous.

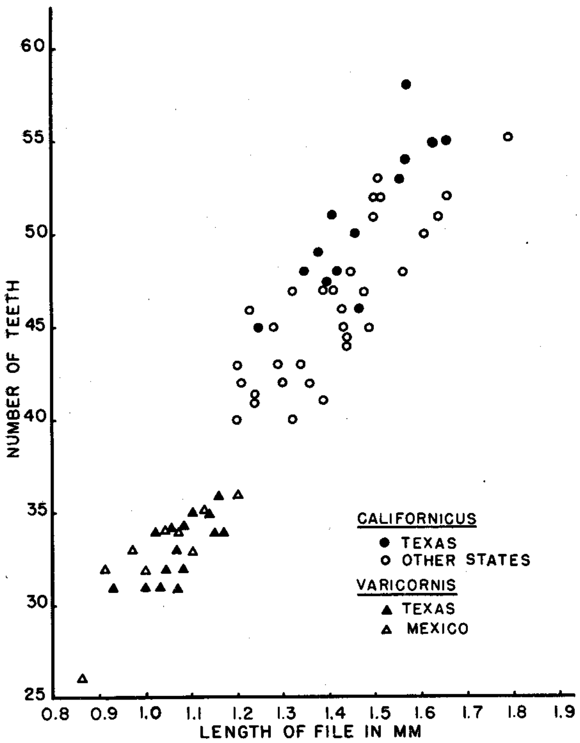

FIG. 15.—Scatter diagram showing separation of *Oecanthus californicus* and *O. varicornis* by characteristics of the stridulatory file. Specimens of *californicus* from seven states other than Texas and specimens of *varicornis* from five Mexican states are included.

The only other feature found useful in separating *varicornis* and *californicus* is size. *Varicornis* averages larger in all dimensions than *californicus*, there being no obvious differences in proportions. For example, the following measurements are a comparison of 11 males of *varicornis* from five localities in Texas with 12 males of *californicus* from six localities in Texas. All measurements are in millimeters, and in each case the figures for *californicus* are in italics and follow those for *varicornis*. Length of pronotum, 2.4 - 2.8 (average 2.63), *2.1 - 2.5* (*2.28*); greatest width of dorsal field of pronotum, 2.5 - 2.8 (2.67), *2.1- 2.6* (*2.35*); length of tegmen, 12.1 - 13.8 (13.0), *10.7 - 12.5* (*11.6*); width of dorsal field of tegmen, 5.7 - 6.7 (6.3), *5.0 - 6.3* (*5.8*); length of hind femur, 8.0 - 9.4 (8.7), *7.2 - 8.8* (*8.0*).

CALLING SONGS

Each of the three species in the *varicornis* group produces a calling song which is a continuous trill.

Figure 16 shows the relationship between pulse rate and temperature demonstrated for Ohio specimens of *latipennis*. Recordings made in the field in Ohio, Kentucky, Tennessee (Dyer County), and Virginia (Chesterfield County) exhibit the same relationship.

The pulse-rate-temperature relationships for *californicus* are shown in figure 17. Although only a few recordings were available for analysis, it seems that *californicus* from Idaho and California does not differ appreciably in pulse rate from *latipennis*. Only the recordings from Palo Pinto County, Texas, show an appreciable difference, and these fall well below the regression line for *latipennis*.

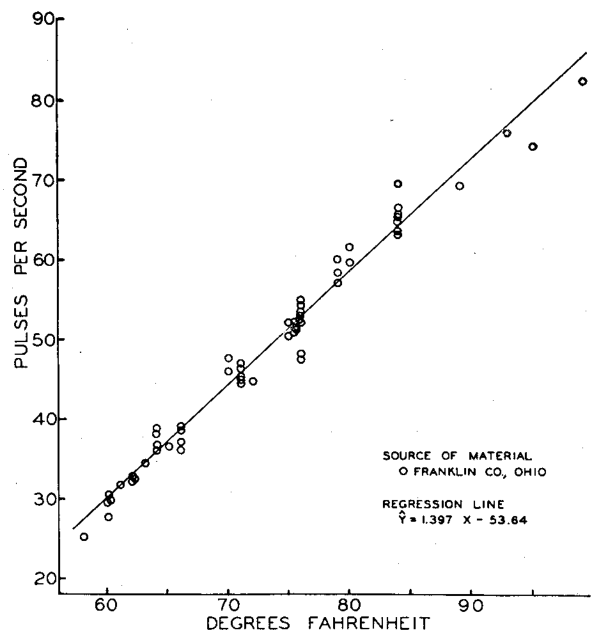

FIG. 16.—Effect of temperature on pulse rate in *Oecanthus latipennis*, laboratory recordings.

The songs of *californicus* and *latipennis* may be distinguished by the relationship between pulse rate and frequency (fig. 5). At a given pulse rate the song of *californicus* is considerably higher in frequency than that of *latipennis*. The recordings of *californicus* from Palo Pinto County, Texas, had an even higher frequency (about 3,500 cps at 35 p/s) than those from farther west, which are represented in figure 5.

The song of *varicornis* is known as a continuous trill from field notes by I. J. Cantrall, J. J. Friauf, and T. J. Cohn. No tape recordings are available for analysis, but on the basis of the file structure it is probable that the pulse rate at a given temperature is markedly higher in *varicornis* than in *californicus* or

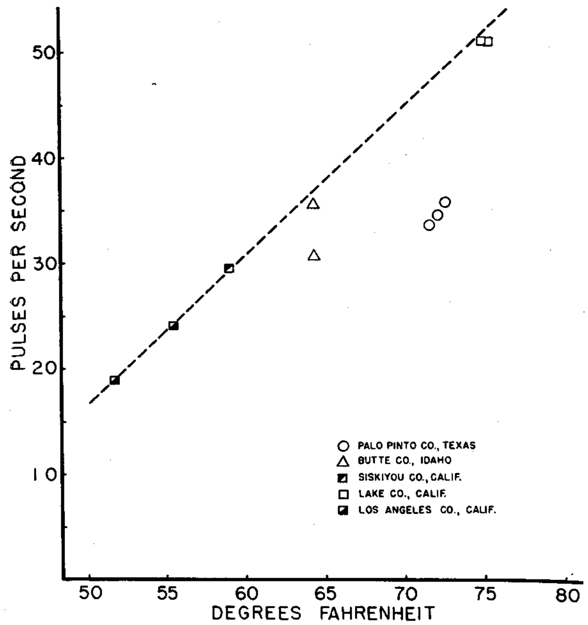

FIG. 17.—Effect of temperature on pulse rate in *Oecanthus californicus*, field recordings. The dotted line is the regression line for *latipennis* (fig. 16).

latipennis. Ordinarily in similar species the fewer the file teeth, the faster the pulse rate.

The slower pulse rate of *californicus* in Texas may be a result of occasional contact with *varicornis* and *latipennis*. In such a situation there would be selection toward a more unique calling song, and if *varicornis* is faster than *latipennis*, slowing of pulse rate is the most likely effect on *californicus*.

DISCUSSION

The three species of the *varicornis* group have probably evolved relatively recently. They are quite similar morphologically and are not known to overlap in their distributions. That they are reproductively isolated is evidenced by their characteristics in eastern Texas where their ranges are contiguous. Here the species are as distinct as anywhere in their ranges. Indeed in terms of song characters (at least for *latipennis* and *californicus*) and file characters, the Texas populations show greater differences than those from areas more widely separated. If distinct species were not involved, the opposite relationship (intergradation) would be expected.

Mexican and Central American specimens of the *varicornis* group apparently include one or more additional species.

ACKNOWLEDGEMENTS

During the past seven years, many persons have contributed to this study by collecting specimens, by giving access to collections and field notes, by the loan of specimens including types, and in innumerable other ways. Without their efforts, this revision could not have been completed.

I especially wish to acknowledge the invaluable assistance and advice of the following persons: Dr. R. D. Alexander of the University of Michigan Museum of Zoology, for the loan of specimens, recordings, and notes, for many helpful suggestions, and for reviewing this manuscript; Dr. Ashley B. Gurney, U. S. Department of Agriculture, for the loan of specimens, for assistance in borrowing types, for taxonomic advice, and for reviewing this manuscript; Dr. T. H. Hubbell of the University of Michigan Museum of Zoology, Dr. E. S. Thomas of the Ohio State Museum, Columbus, and J. A. G. Rehn of the Academy of Natural Sciences of Philadelphia, for the loan of specimens and field notes and for advice on nomenclatural problems.

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Reprinted from the
ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA
Volume 55, Number 3, pp. 303-322 May, 1962